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Spatially Structured Continuous-Time Markov Population Models

Final Report

Spatially Structured Continuous-Time Markov Population Models

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The Problem

Patch-occupancy metapopulation models have evolved from the early analytical models of Markov processes used to gain qualitative insights about persistence threshold behavior of hypothetical populations in fragmented habitat complexes. Finite mathematical extensions are being used increasingly as prescriptive models to identify the most important and critical number of patches as decision aids for conservation of real populations. This applied use of these models motivates questions about the degree to which key simplifying assumptions might affect prescriptive recommendations.

Specific Questions

The purpose of this line of investigation is to examine the combined effect on rankings and the critical number of patches (or persistence inferences) arising from three assumptions commonly used in patch-occupancy metapopulation models:

1. Quasi-steady state assumptions,
2. Constant local extinction and colonization probabilities, and
3. Constant-abundance patch-occupancy state variables.

Methods

Moment-differential equations matched with first and second moments are being derived to approximate exact Kolmogorov forward equations of a Markov metapopulation system, with populations in fragmented habitats modeled at three increasingly coarse levels of detail (or "scale"):

1. Territory-level occupancy,

2. Patch-level abundance, and
3. Patch-level occupancy.

Numerical integration from a set of initial conditions of approximation models for each of these scales will allow us to individually relax the three assumptions described above.

For a given habitat complex (depicted as a binary landscape), marginal rankings of patches based on overall probability of persistence can be determined from our moment differential models at each scale by removing individual patches from the complex in turn. Initially, we will explore scale effects qualitatively by varying single landscapes in a variety of ways (e.g., amount of habitat, spatial autocorrelation of habitat, average patch size, size of largest patch, average distance between patches, etc.). Monte Carlo simulations might also be used to quickly identify landscapes with persistence probability responses of particular interest (e.g., near "threshold"). If scale effects are observed, then we will consider developing an experimental design for quantitative analysis.

Status

By last spring, Prof. Taaffe had derived Kolmogorov forward equations for both occupancy and abundance models that can be used at either the territory or patch scale, as set by the choice of parameter values. These models require $(c+1)^k$ equations for k land units of c capacity each. The moment-differential abundance model matched with first moments was also derived and coded in the Maple 7 programming language (see Appendix 1), and a report (see Appendix 2) and a powerpoint presentation (see Appendix 3) were prepared. This model requires k equations for k land units, making them much

more tractable for analysis. This work was described in an invited presentation at the International Federation of Operational Research Society's Symposium on Models and Systems in Forestry held in Punta de Tralca, Chile, March 4-7, 2002 ("Spatially explicit Markov models for designing habitat reserves," Bevers, M., M.R.Taaffe, L. Travis and C.H. Flather).

Last summer at a meeting in Fort Collins, Prof. Taaffe derived the second-moment differential equation model matched with first and second moments, and a series of comparative experiments were designed jointly (Fig. 1). Last fall some preliminary analysis was completed for a three-patch system using the Kolmogorov forward equations derived earlier. A second powerpoint presentation describing this analysis (see Appendix 4) was subsequently prepared and presented at the Institute for Operations Research and the Management Sciences national convention in San Jose, California, November 17-20, 2003 ("Markov models of endangered species population and habitat," Travis, L., M.R. Taaffe, M. Bevers and C.H. Flather). Work with the second-moment differential equation model was not finished in time for this conference.

More work is needed to review, program and test the second-moment equation system before the comparative analyses shown in Fig. 1 can be completed. However, last September Prof. Taaffe moved from the University of Minnesota to Virginia Polytechnic and State University (Virginia Tech). We plan to complete this work through new agreements with that institution:

1. Both models will be revised to allow birth rates that vary by land unit in order to allow seasonal reproduction and maturation of offspring. This will be modeled by the use of "nursery" land units paired with "adult" land units, combined with seasonal rate changes invoked at predetermined times throughout the numerical integration.
2. Expected occupancy by territory and overall extinction probability as calculated with the approximation model for a small (10-20 territory) problem will be compared to the same outputs from the exact model as a validation test.
3. Persistence threshold behavior will be explored by projecting extinction probabilities over time from initially occupied territories in single patches of increasing size that are roughly circular (or perhaps square) in shape. Similarly, total expected abundance will be calculated for these patches over a range of habitat quality levels (e.g., reflected by greater patch capacities, higher birth rates, lower mortality rates, etc.).
4. Occupancy- vs. abundance-based patch rankings will be compared as previously described.

As future work, we have also discussed choosing data collection and modeling methods (i.e., occupancy vs. abundance and patch- vs. territory-level) based on acquisition cost and the value of the information obtained. We have also discussed the possibility of further extensions to the approximation model to account for random disturbances and for multiple (probably competing) species.

Schedule

Funds committed to the research joint venture agreement (RJVA) for this project were exhausted this summer and the agreement has expired. This timing coincided with Prof. Taaffe's move from Minneapolis to Virginia. The products documented here are the final products of this RJVA. Any future funding for related research will be set up through our new RJVA with Virginia Tech.

Model	Method			
	Hanski's Incidence Model	Moment Matching	Kolmogorov Forward Eq.	Simulation
Territory Occupancy (most ecologically realistic)		4	5	This represents a yet-to-be-designed simulated management experiment. It may have the following steps: (1) simulate population data; (2) monitor and estimate parameters under patch occupancy model; (3) monitor and estimate parameters under territory occupancy model; (4) analyze data under both patch occupancy and territory occupancy models; (5) recommend / pick a "best" layout under patch occupancy and territory occupancy models; (6) implement the recommendation and simulate the effectiveness of each recommendation.
Patch Abundance		3		
Patch Occupancy	1	2	6	

4 — 5	Step 1: Validate that moment matching will work with small capacities (cap = 1.0).
2 — 6	This validation is unnecessary since the 4 — 5 comparison is numerically identical
3 2	Does abundance matter?
3 6	Also asks if abundance matters but is done so with a "toy" comparison since KF can't deal with large problems (i.e., large number of patches). *Do we really need to do this one?*
4 3	Does within patch resolution matter?
1 2	Does steady state (or quasi-steady state) matter?

Fig. 1

Appendix 1

Copyright: Michael Bevers, Kurt Flather, Laurel Travis, and Michael Taaffe - 2001
Created: 08/15/01
Updates: 08/15/01 02/10/02 02/12/02 02/13/02 02/14/02 02//15/02

This is a Maple 7 worksheet to evaluate the first moment for the ferret population level in each of k patches.

Inputs

k = number of territories
Init_ferrets(k,k) = initial number of ferrets in territory k
beta = dispersal rate per ferret
mu(k,k) = death rate per ferret in territory k
theta (k) = migration rate per ferret in territory k
alpha(k,k) = conditional probabilities of a ferret dispersing from territory i to territory j, given there is a dispersal from territory i
gamma(k,k) = conditional probabilities of a ferret migrating from territory i to territory j, given there is a migration from territory i

Outputs

M1[k](t) = Expected number of ferrets in territory k at time t

```
> Restart:
> with(plots):
> with(DEtools):
> k :=3; ***** ENTER the number of patches here *****
```

$$k := 3$$

```
> Init_ferrets := vector(k,[125,45,5] ); ***** Enter the number of ferrets at time t=0 for each of the k patches here *****
```

$$Init_ferrets := [125, 45, 5]$$

```
> c := vector(k,[250,90,10] ); ***** Enter the carrying capacity of each territory *****
```

$$c := [250, 90, 10]$$

```
> beta(t) := 1.8 + .6 * sin( evalf(Pi) * t/ 5 ); ***** Enter the per-ferret birth rate here *****
```

$$\beta(t) := 1.8 + .6 \sin(.6283185308\, t)$$

```
> mu := vector(k,[.4,.4,.4]); ***** Enter the death rate for each of the k patches here *****
```

$$\mu := [.4, .4, .4]$$

```
> theta := vector(k,[.868, 1.352, 3.570]); *** Enter the migration
```

rate per ferret per territory here *****

$$\theta := [.868,\ 1.352,\ 3.570]$$

```
> alpha := matrix(k,k,[.68392,.00165,.00001,
.00507,.52277,.00090,   .00016,.00865,.24431] );
```

***** Enter the conditional probabilities for newly hatched ferrets dispersing from patch i to patch j here *****

$$\alpha := \begin{bmatrix} .68392 & .00165 & .00001 \\ .00507 & .52277 & .00090 \\ .00016 & .00865 & .24431 \end{bmatrix}$$

```
> gama := matrix(k,k,[.0,.00522,.00003, .01062,.0,.00189,
.00021,.01145,.0] );
```

***** Enter the migration conditional probabilities for ferrets migrating from patch i to patch j here *****

$$gama := \begin{bmatrix} 0. & .00522 & .00003 \\ .01062 & 0. & .00189 \\ .00021 & .01145 & 0. \end{bmatrix}$$

```
> M1 := array(1..k);
```

$$M1 := \text{array}(1 .. 3, [\ ])$$

We now enter the moment differential equations...

```
> for j from 1 to k do
>     dd[j] := 0:
>     for r from 1 to k do:
>         p     := 1 - ( evalf(M1[r](t)/c[r]) )^c[r];
>         dd[j] := dd[j] + theta[r]*gama[r,j]*M1[r](t)*p +
beta(t)*alpha[r,j]*M1[r](t)*p;
>     od;
>     Moment_1[j] := diff(M1[j](t),t) = dd[j] -
mu[j]*M1[j](t) - theta[j]*M1[j](t);
>     Init_Cond[j] := M1[j](0) = Init_ferrets[j];
> od:
> Moment_1_set :=  seq(Moment_1[j], j=1..k):
> IC_set       :=  seq(Init_Cond[j],j=1..k):
```

dsolve/numeric/IVP - find numerical solution of ODE initial value problems

Calling Sequence

dsolve(odesys, numeric, vars, options)

dsolve(numeric, vars, procopts, options)

Parameters

odesys - set or list; ordinary differential equation(s) and initial conditions
numeric - name; instruct dsolve to find a numerical solution
vars - (optional) dependent variable or a set or list of dependent variables for odesys
procopts - (required if odesys is not present) options that specify a procedure defined system
options - (optional) equations of the form keyword = value

```
> sol := dsolve( {Moment_1_set} union {IC_set}, numeric,
range=0..300);
```

$$sol := \text{proc}(rkf45_x) \ \ldots \ \text{end proc}$$

```
> sol(0);
```

$$[t = 0., M1_1(t) = 125., M1_2(t) = 45., M1_3(t) = 5.]$$

```
> sol(50);
```

$$[t = 50., M1_1(t) = 12.7083037689427982, M1_2(t) = .122668702920210218,$$
$$M1_3(t) = .000303524792223786305\ ]$$

plots[odeplot] - 2-D or 3-D plot of output from dsolve

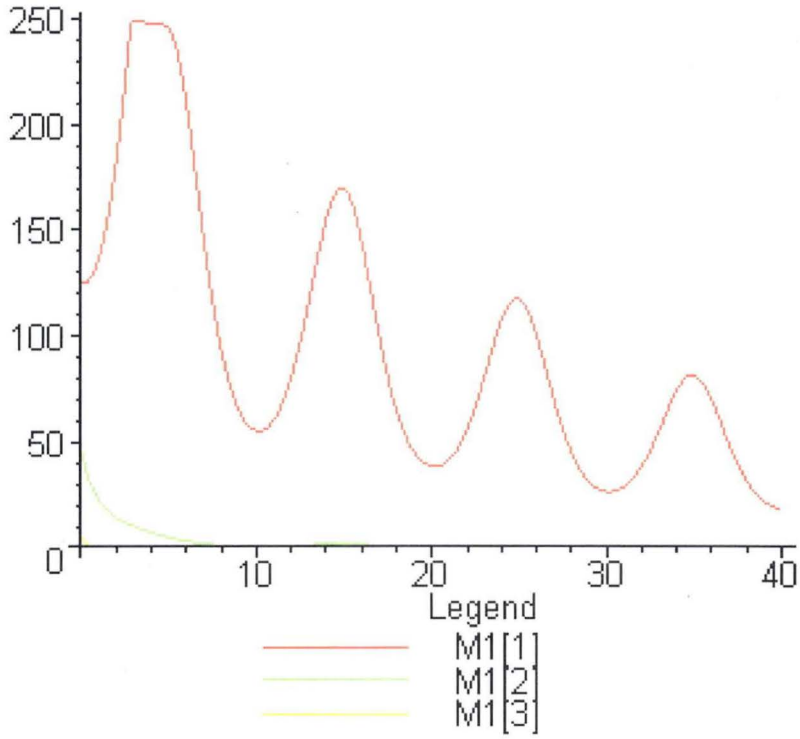
Calling Sequence

odeplot(s, vars, range, options);

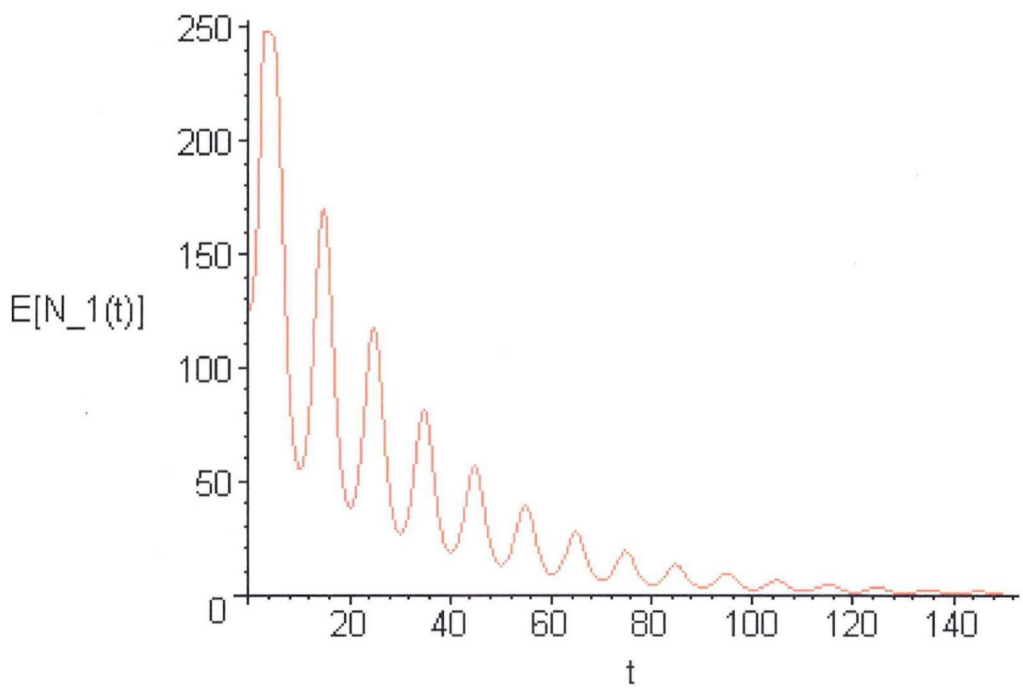
Parameters

s - output from a call to dsolve(... , numeric)
vars - (optional) variables to specify ordering of axes
range - (optional) parameter specification of type a..b
plot options - (optional) plot options; see ?plot[options]

```
> odeplot(sol, [ [t,M1[1](t)],[t,M1[2](t)],[t,M1[3](t)] ],
0..40 );
```

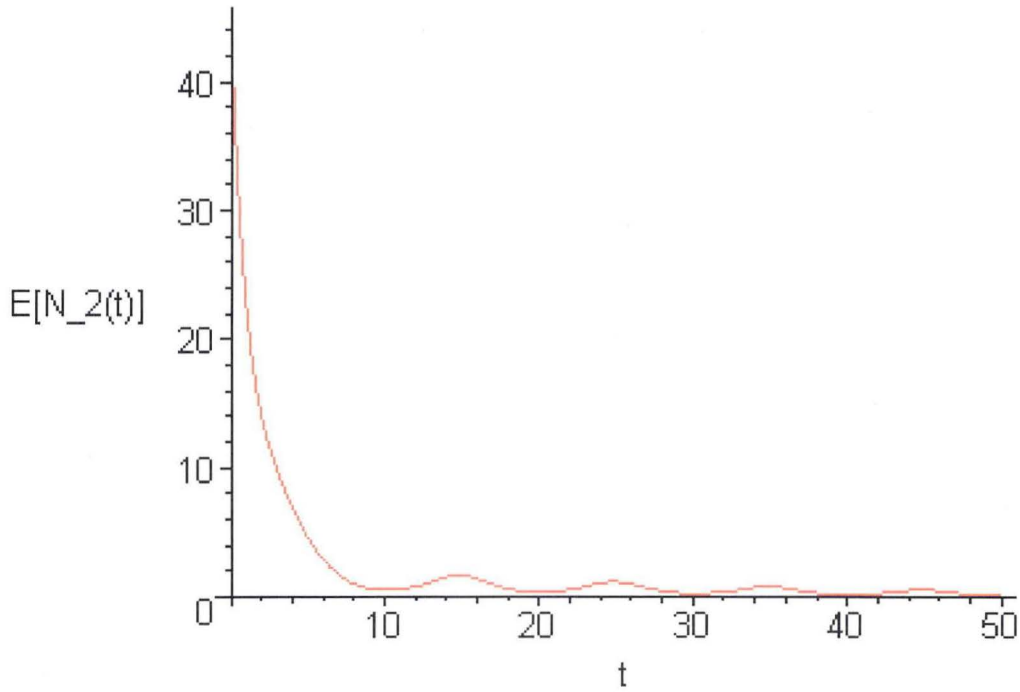



```
> odeplot(sol, [t,M1[1](t)], 0..150,
labels=["t","E[N_1(t)]"] );
```

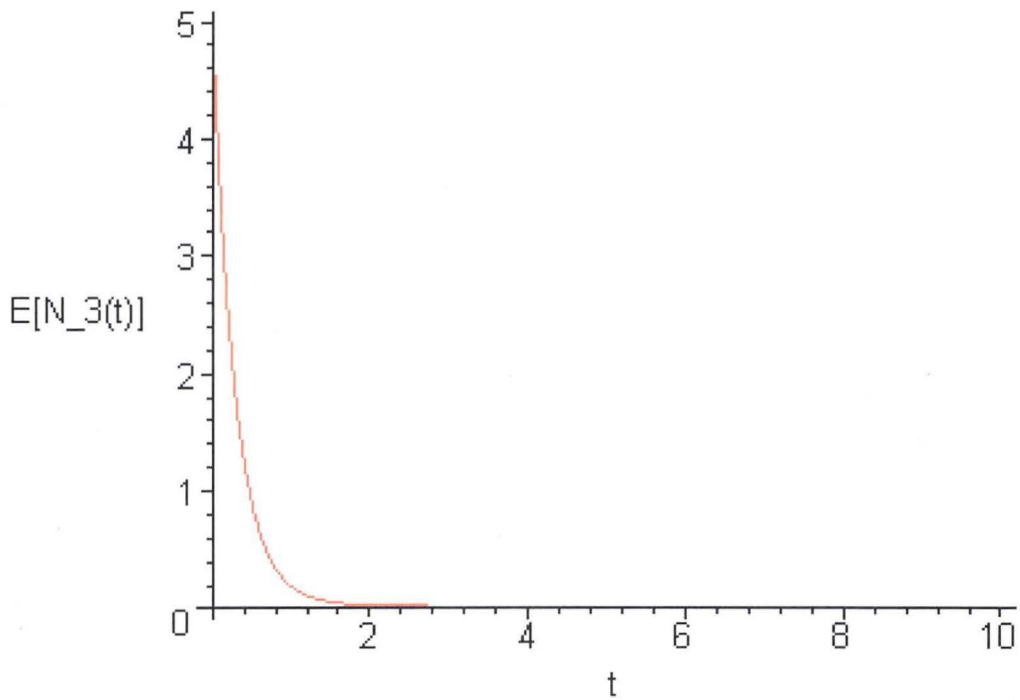



```
> odeplot(sol, [t,M1[2](t)], 0..50, labels=["t","E[N_2(t)]"]
```

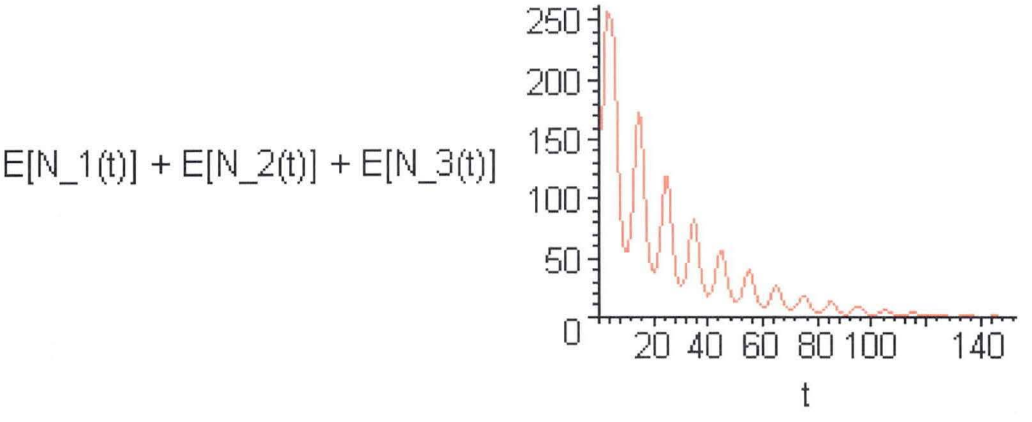
```
);
```



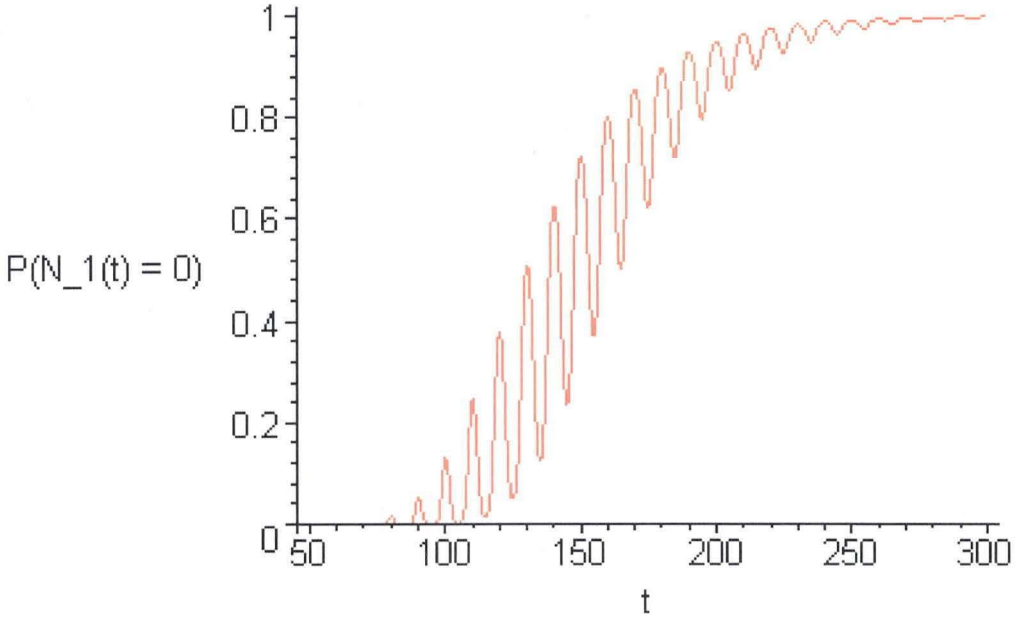

```
> odeplot(sol, [t,M1[3](t)], 0..10, labels=["t","E[N_3(t)]"]
);
```



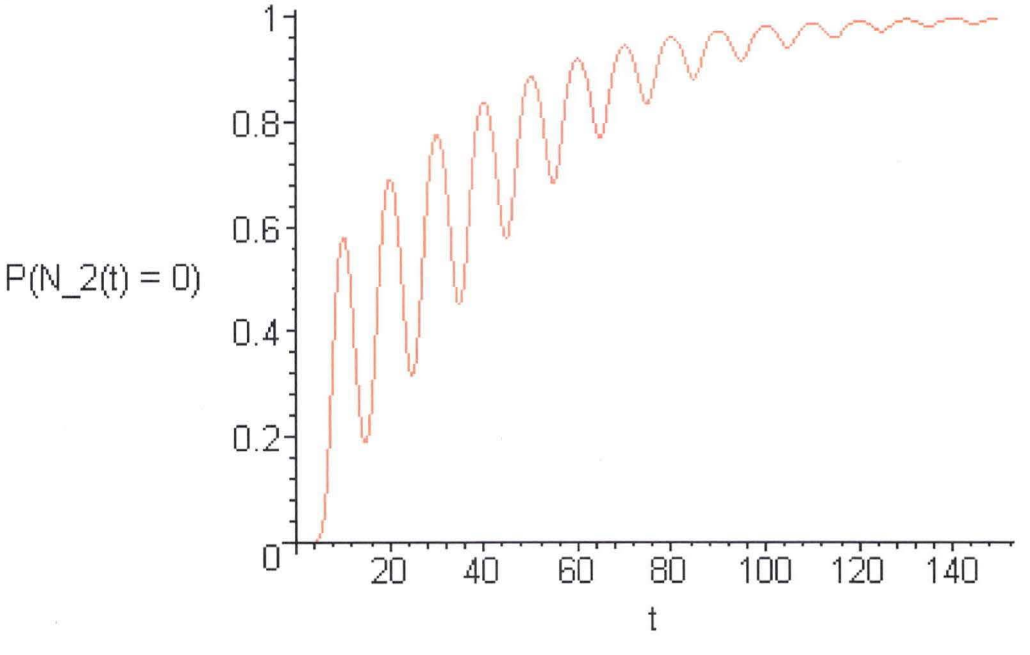
```
> odeplot(sol, [t, (M1[1](t)+M1[2](t)+M1[3](t)) ], 0..150,
labels=["t","E[N_1(t)] + E[N_2(t)] + E[N_3(t)]"]);
```




```
> odeplot(sol, [t,  (1- M1[1](t)/c[1])^c[1] ] , 50..300,
labels=["t","P(N_1(t) = 0)"]);
```

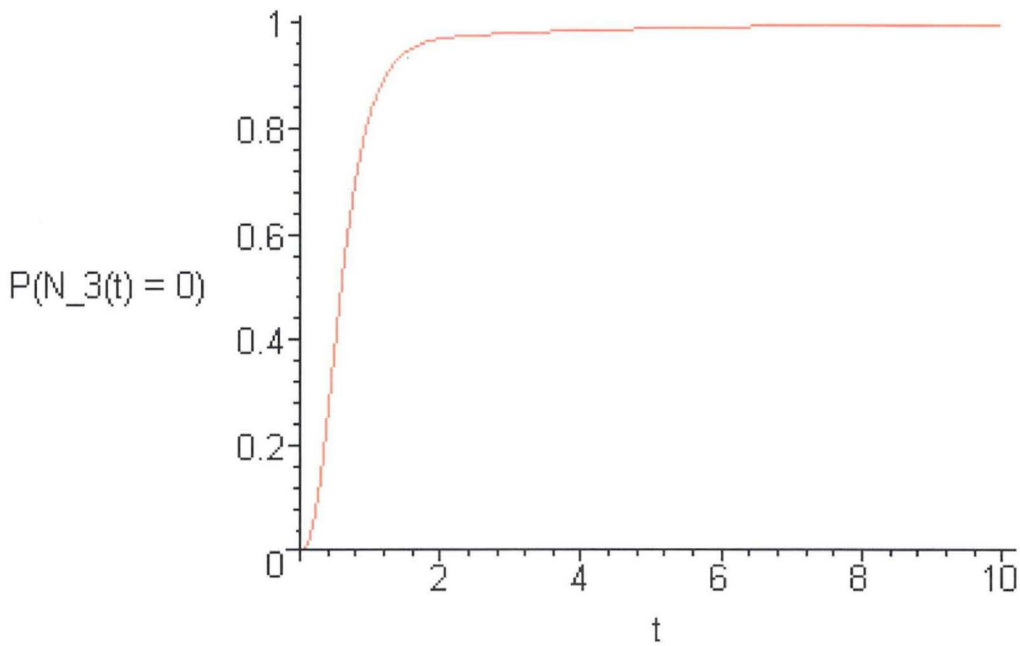



```
> odeplot(sol, [t,  (1- M1[2](t)/c[2])^c[2] ] , 0..150,
labels=["t","P(N_2(t) = 0)"]);
```

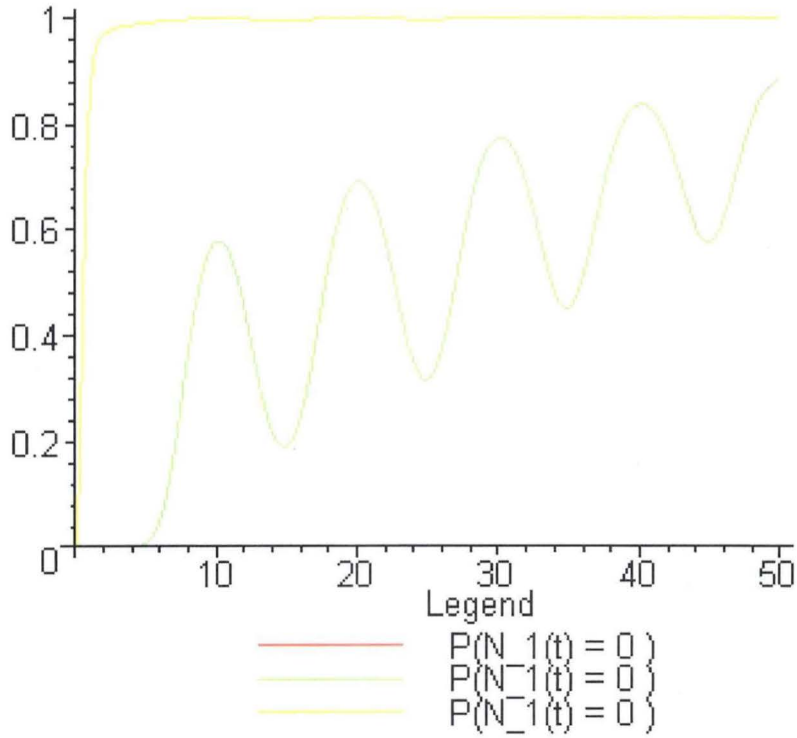



```
> odeplot(sol, [t,  (1- M1[3](t)/c[3])^c[3] ] , 0..10,
```

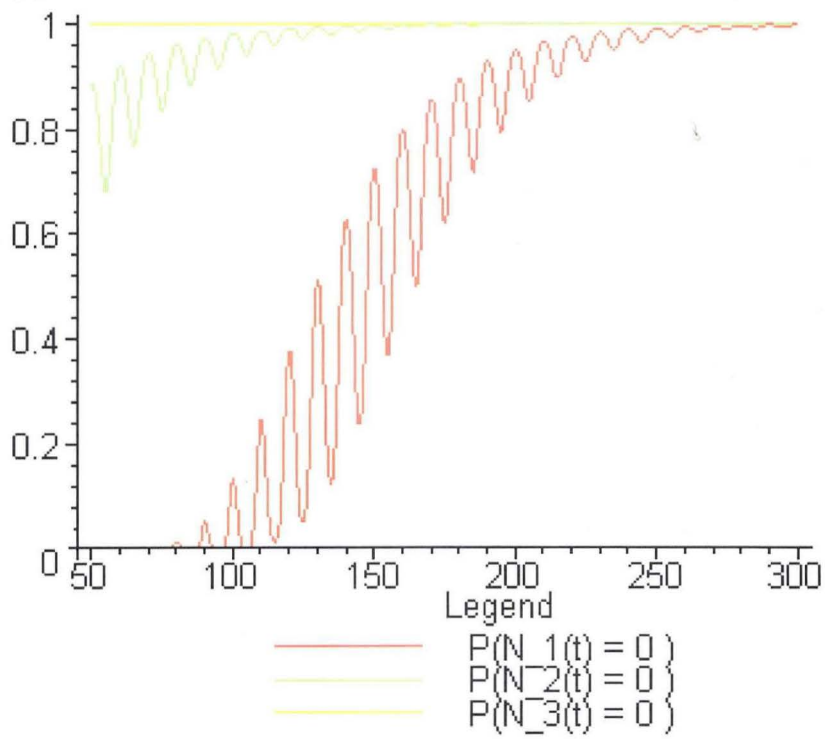
```
labels=["t","P(N_3(t) = 0)"]);
```




```
> odeplot(sol, [ [t,(1-M1[1](t)/c[1])^c[1]   ], [t,(1-
M1[2](t)/c[2])^c[2] ], [t,(1-M1[3](t)/c[3])^c[3]   ] ],
0..50 );
```




```
> odeplot(sol, [ [t,(1-M1[1](t)/c[1])^c[1]   ], [t,(1-
M1[2](t)/c[2])^c[2] ], [t,(1-M1[3](t)/c[3])^c[3]   ] ],
50..300 );
```



Appendix 2

A Continuous-Time Markov Process for Species Survival

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1. Backgound ... Introduction ... Problems with deterministic models of small-population models...

2. The occupancy model

In this section we define the notation for our stationary, continuous-time Markov-process model of species survival.

Definitions:

1. $\mathcal{N} \equiv \{\mathbf{N}(t); t \geq 0\}$ where $\mathcal{N}$ is the random process, and $\mathbf{N}(t)$ is a random vector at time t representing the state of the system, and
   $\{\mathbf{N}(t); t \geq 0\} \equiv \{[N_k(t), \cdots, N_1(t),], t \geq 0\}$, where $N_i(t) = 0, 1,$
   $i = 1, \cdots, k$ is the $k-$dimensional representation of the random process.
2. $N_i(t) \equiv \left\{ \begin{array}{l} 0, \text{ if "territory" } i \text{ is not "populated" at time } t \\ 1, \text{ if "territory" } i \text{ is "populated" at time } t \end{array} \right\}$, for $i = 1, \cdots, k$.

3. $k \equiv$ number of territories.

4. $\mathbf{X} \equiv \{X(t) : t \geq 0\}$, where $X(t) = 0, 1, \cdots, m-1$ is the natural-number representation of the binary number resulting from concatenating the values of the $N_i(t)$ random variables in decreasing order of territory number. For example $X(t) = 13 \Leftrightarrow 1101$ in binary; thus $X(t) = 13 \Leftrightarrow [N_4(t) = 1, N_3(t) = 1, N_2(t) = 0, N_1(t) = 1]$. In all that follows, time is measured in *years*.

5. $P_{n_k \cdots n_1}(t) \equiv \Pr\{N_k(t) = n_k, \cdots, N_1(t) = n_1\}$.

6. $P_{n_k \cdots n_1}(t)' \equiv \frac{d}{dt} P_{n_k \cdots n_1}(t)$.

7. $P_x(t) \equiv \Pr\{X(t) = x\}$.

8. $P_x(t)' \equiv \frac{d}{dt} P_x(t)$.

9. $\mu_l \equiv$ populated territory l "death" rate.

10. $\beta \equiv$ "dispersal" rate from an occupied territory.

11. $\alpha_{ij} \equiv$ conditional probability that a disperser goes to territory j given there is a dispersal from territory i, $i = 1, \cdots, k$, $j = 1, \cdots, k$, and $\alpha_{ii} \equiv 0$. Observe that $\sum_{j=1}^{k} \alpha_{ij} \leq 1$, for $j = 1, \cdots k$.

12. $\alpha_{io} \equiv$ conditional probability that a disperser goes to an uninhabitable territory (territory o) given there is a dispersal from territory i, $i = 1, \cdots, k$ (for example a newly hatched creature leaves territory i and decides to set up house in a tar pit). Observe that $\alpha_{jo} = 1 - \sum_{j=1}^{k} \alpha_{ij}$, for $j = 1, \cdots k$. (Also observe that there is no need to represent the occupancy or lack of occupancy of territory o because it is never occupied).

13. $\theta \equiv$ migration rate from an occupied territory.

14. $\gamma_{ij} \equiv$ conditional probability that an occupant migrates to territory j given there is a migration from territory i, $i = 1, \cdots, k$, $j = 1, \cdots, k$, and $\alpha_{ii} \equiv 0$. Observe that $\sum_{j=1}^{k} \gamma_{ij} \leq 1$, for $j = 1, \cdots k$.

15. $\gamma_{io} \equiv$ conditional probability that an occupant of territory i migrates to an uninhabitable territory (territory o) given there is a migration from territory i, $i = 1, \cdots, k$ (for example momma creature leaves territory i and decides to set up house in a tar pit). Observe that $\gamma_{jo} = 1 - \sum_{j=1}^{k} \gamma_{ij}$, for $j = 1, \cdots k$.

16. $m \equiv 2^k \equiv$ the number of states in the state space.

17. $b(x) \equiv \texttt{BINARY}[x]$, and $b^{-1}(\cdot)$ is the inverse binary function.

18. $b_i(x) \equiv i^{th}$ digit, from the right, of the binary representation of the natural number x.

We represent the random state of the system at time t in two equivalent ways; the $k-$dimensional Bernoulli random variable $\mathbf{N(t)}$ and the single-dimensional random variable $X(t)$. For $X(t) = \mathbf{N}(t)$ we mean that each of the binary digits of $b\,(X(t))$, from left to right, have the same value as the variables $N_k(t), \cdots, N_1(t)$, respectively, and, equivalently, $b^{-1}\,(N_k(t)|\cdots|N_1(t)) = X(t)$, where the operator | represents concatenation.

For example in a system having $k = 4$ territories, the number of states is $m = 16$, and at time t the state $X(t) = 13$ in binary is 1101, and $b(13) = 1101$, or

$$b_4(13) = 1, b_3(13) = 1, b_2(13) = 0, b_1(13) = 1,$$

and $b^{-1}(1101) = 13$, which corresponds to $\mathbf{N}(t) = [N_4(t) = 1, N_3(t) = 1, N_2(t) = 0, N_1 = 1]$.

2.1 The Kolmogorov forward equations

For the $k-$territory species-survival model, we present the Kolmogorov forward differential difference equations using both the natural-number and the $k-$dimensional binary-number

representations.

$$
\begin{aligned}
P_x(t)' &= -\left(\sum_{i=1}^{k} b_i(x)(\mu_i+\theta) + \beta\sum_{i=1}^{k}(1-b_i(x))\sum_{\substack{j=1\\ j\neq i}}^{k} b_j(x)\alpha_{ji}\right)P_x(t) \\
&+\beta\sum_{j=1}^{k} b_j(x)\sum_{\substack{i=1\\ i\neq j}}^{k} b_i(x)\alpha_{ji}P_{b^{-1}[b_k(x)|\cdots|1-b_i(x)|\cdots|b_1(x)]}(t) \\
&+\theta\sum_{j=1}^{k}(1-b_j(x))\sum_{\substack{i=1\\ i\neq j}}^{k} b_i(x)\gamma_{ji}P_{b^{-1}[b_k(x)|\cdots|(1-b_j(x))|\cdots|1-b_i(x)|\cdots|b_1(x)]}(t) \\
&+\sum_{j=1}^{k}(1-b_j(x))\mu_j P_{b^{-1}[b_k(x)|\cdots|1-b_j(x)|\cdots|b_1(x)]}(t)
\end{aligned}
$$

for $x = 0, \cdots, m-1$.

Comments: The negative flux in this differential difference equation represents all of the possible ways for the system to leave state x – via deaths or successful new dispersals. The positive flux represents the ways to enter state x – via deaths or new dispersals.

While this representation is compact and perhaps easiest to code, the more natural $k-$tuple representation is easier to interpret. For the $k-$tuple representation of the random state of the system we have:

$$
\begin{aligned}
P_{n_k\cdots n_1}(t)' &= -\left(\sum_{l=1}^{k} n_l(\mu_l+\theta) + \beta\sum_{l=1}^{k}(1-n_l)\sum_{\substack{j=1\\ j\neq l}}^{k} n_j\alpha_{j,l}\right)P_{n_k\cdots n_1}(t) \\
&+\beta\sum_{l=1}^{k} n_l\sum_{\substack{r=1\\ r\neq l}}^{k} n_r\alpha_{rl}P_{n_k\cdots(1-n_l)\cdots n_1}(t) \\
&+\theta\sum_{l=1}^{k} n_l\sum_{\substack{r=1\\ r\neq l}}^{k}(1-n_r)\gamma_{rl}P_{n_k\cdots(1-n_r)\cdots(1-n_l)\cdots n_1}(t) \\
&+\sum_{l=1}^{k}(1-n_l)\mu_l P_{n_k\cdots(1-n_l)\cdots n_1}(t)
\end{aligned}
$$

We can also express this set of differential-difference equations in matrix form.

$$\mathbf{P}(t)' = \mathbf{P}(t)\mathbf{Q},$$

where

$$\mathbf{P}(t) \equiv (\Pr\{X(t) = 0\}, \cdots, \Pr\{X(t) = k\}) = (\Pr\{\mathbf{N}(t) = 00\cdots0\}, \cdots, \Pr\{\mathbf{N}(t) = 11\cdots1\})$$

is the $1 \times k$ vector of state probabilities, $\mathbf{P}(t)'$ is the $1 \times k$ vector of state-probability derivatives, and $\mathbf{Q}$ is the infinitesimal generator for the Markov process.

3. Solution methods

The above set of equations comprise a set of simple, linear, first-order differential-difference equations and can be evaluated in several different ways. In the usual case of stationary, continuous-time Markov processes a modeler is often most interested in the *steady-state*, or equilibrium behavior of the system. Equilibrium occurs when the state probabilities are no longer changing with time – so the *system* that is in steady state is the system of uncertainty.

In the case of species-survivor Markov models, the steady-state probabilities are not of interest; in fact, the steady-state distribution of the system state is trivial and

$$\lim_{t\to\infty} X(t) \to 0,$$

in distribution. This is reasonable model behavior since in the infinite future the species will go extinct, almost surely. So the state $X(t) = 0$, or the binary equivalent $\mathbf{N}(t) = (000\cdots0)$, is an *absorbing* state; i.e., once the system enters the *extinct* state it cannot leave that state, "Jurrasic Park" notwithstanding. Also, for our model there is exactly *one* absorbing state (extinct is extinct).

For Markov species-survival models, a performance measure of interest are *transient* probabilities of species survival by time τ (typically $\tau = 100$) years. We will define

$$F_\tau \equiv \Pr\{X(\tau) > 0\} \equiv \Pr\{X(\tau) \neq 0\} \equiv \Pr\{\mathbf{N}(\tau) \neq \mathbf{0}\}$$

$$= \quad 1 - \Pr\{X(\tau) = 0\} \equiv 1 - \Pr\{\mathbf{N}(\tau) = \mathbf{0}\}$$

where $\mathbf{0}$ is a vector of zeroes.

For Markov processes having a finite number of states and having exactly one absorbing state we define the time-till-absorption random variable to be T. Let $F_T(t) \equiv \Pr\{T \leq t\}$; thus $F_\tau \equiv 1 - F_T(\tau)$. The random variable T is called a *phase-type* random variable and is a special case of the more general *first-passage-time* random variable for Markov processes. There are several methods of examining the behavior of these phase-type distributions.

3.1 The matrix-analytic method

The matrix-analytic or matrix-geometric is analytic in that we have a nice expression for the phase-type distribution function (and the power moments, and Laplace transform...). The solution does require computation of a matrix exponential. The form of the phase-type distribution function involves the infinitesimal generator of the Markov process (or the "rate matrix" or the process kernel). The generator, $\mathbf{Q}$ of the Markov process is easily formed from the set of Kolmogorov equations given above (THIS WILL BE DONE EXPLICITLY LATER AND PLACED IN THIS SECTION. Let $\mathbf{Q}$ be the generator associated with our set of Kolmogorov equations, and let

$$\mathbf{Q} = \left[\begin{array}{c|c} \mathbf{Q}_1 & \mathbf{Q}^o \\ \hline \mathbf{0} & 0 \end{array}\right]$$

where $\mathbf{Q}_1$ is the $(k-1) \times (k-1)$ submatrix of transition rates from transient-to-transient states, $\mathbf{Q}^o$ is the $(k-1)\times 1$ submatrix of transition rates from transient states to the absorbing state ("extinct" or $\mathbf{N}(t) = (000\cdots0)$), and $\mathbf{0}$ is the $(k-1)$ dimensional vector of zeroes.

The distribution function for the time-till absorption is then

$$\Pr\{T \leq t\} \equiv F_T(t) = 1 - \boldsymbol{\alpha} \exp(\mathbf{Q}_1 t)\, \mathbf{e},$$

for all $t \geq 0$, where $\boldsymbol{\alpha}$ is defined as the $(k-1)$ dimensional vector, $(\alpha_1, \cdots, \alpha_{k-1})$, containing

the initial-state probabilities at time $t = 0$; i.e., $\Pr\{X(t) = i\} \equiv \alpha_i$ and $\sum_{i=0}^{k-1} \alpha_i = 1$, and $\mathbf{e}$ is a $1 \times (k-1)$ vector of 1's.

And from earlier we see that

$$F_\tau = F_T(\tau),$$

for $\tau \geq 0$.

But of course matrix-exponential computations present computational challenges....

3.2 Numerical evaluation of matrix exponentials

3.3 The Laplace transform method

3.3.1 The Whitt algorithms for numerical inversion of Laplace transforms

3.4 The Eigenvalue/Eigenvector method

3.5 Evaluation via spectral decomposition of the infinitesimal generator

3.6 5^{th}-order Runge-Kutta numerical integration – God's method

4. The time-dependent occupancy model

In this section we define the notation for the time-dependent, continuous-time Markov-process occupancy model of species survival, and list the associated Kolmogorov forward equations. The random variables describing the state of the system at time t are defined above. The only practical method for evaluating the Kolmogorov forward equations numerical integration. Evaluating the K-f equations for the time-dependent case is no more difficult than the stationary case, assuming that the time-dependent rate functions are smooth or integrable.

In order to model the time-dependencies of the nature of the changes taking place in the system we need to define the parameters of the system as function of time.

All definitions are the same as in the previous section with the following time-dependent generalization:

1. $\mu_l(t) \equiv$ populated territory l "death" rate at time t.

2. $\beta(t) \equiv$ "dispersal" rate from an occupied territory at time t.

3. $\alpha_{ij}(t) \equiv$ conditional probability that a disperser goes to territory j given there is a dispersal from territory i, $i = 1, \cdots, k$, $j = 1, \cdots, k$, and $\alpha_{ii}(t) \equiv 0$, at time t. Observe that $\sum_{j=1}^{k} \alpha_{ij}(t) \leq 1$, for $j = 1, \cdots k$.

4. $\alpha_{io}(t) \equiv$ conditional probability that an disperser goes to territory o, an uninhabitable territory, given there is a migration from territory i at time t, $i = 1, \cdots, k$.

5. $\theta(t) \equiv$ migration rate from an occupied territory at time t.

6. $\gamma_{ij}(t) \equiv$ conditional probability that an occupant migrates to territory j given there is a migration from territory i at time t, $i = 1, \cdots, k$, $j = 1, \cdots, k$, and $\gamma_{ii}(t) \equiv 0$. Observe that $\sum_{j=1}^{k} \gamma_{ij}(t) \leq 1$, for $j = 1, \cdots k$.

7. $\gamma_{io}(t) \equiv$ conditional probability that an occupant of territory i migrates to an uninhabitable territory (territory o) given there is a migration from territory i at time t, $i = 1, \cdots, k$.

The Kolmogorov forward equations for the time-dependent $k-$territory species-survival model are:

$$\begin{aligned} P_x(t)' &= -\left(\sum_{i=1}^{k} b_i(x)(\mu_i(t) + \theta(t)) + \beta(t) \sum_{i=1}^{k} (1 - b_i(x)) \sum_{\substack{j=1 \\ j \neq i}}^{k} b_j(x) \alpha_{ji}(t) \right) P_x(t) \\ &\quad + \beta(t) \sum_{j=1}^{k} b_j(x) \sum_{\substack{i=1 \\ i \neq j}}^{k} b_i(x) \alpha_{ji}(t) P_{b^{-1}[b_k(x)|\cdots|1-b_i(x)|\cdots|b_1(x)]}(t) \end{aligned}$$

$$+\theta(t)\sum_{j=1}^{k}(1-b_j(x))\sum_{\substack{i=1\\ i\neq j}}^{k} b_i(x)\gamma_{ji}(t)P_{b^{-1}[b_k(x)|\cdots|1-b_j(x)|\cdots|1-b_i(x)|\cdots|b_1(x)]}(t)$$

$$+\sum_{j=1}^{k}(1-b_j(x))\mu_j(t)P_{b^{-1}[b_k(x)|\cdots|1-b_j(x)|\cdots|b_1(x)]}(t)$$

for $x = 0, \cdots m-1$. And alternatively for the $k-$tuple representation of the random state of the system we have:

$$\begin{aligned}
P_{n_k\cdots n_1}(t)' &= -\left(\sum_{l=1}^{k} n_l(\mu_l(t)+\theta(t)) + \beta(t)\sum_{i=1}^{k}(1-n_l)\sum_{\substack{j=1\\ j\neq l}}^{k} n_j\alpha_{j,l}(t)\right) P_{n_k\cdots n_1}(t) \\
&+\beta(t)\sum_{l=1}^{k} n_l \sum_{\substack{r=1\\ r\neq l}}^{k} n_r\alpha_{rl}(t)P_{n_k\cdots(1-n_l)\cdots n_1}(t) \\
&+\theta(t)\sum_{l=1}^{k} n_l \sum_{\substack{r=1\\ r\neq l}}^{k}(1-n_r)\gamma_{rl}(t)P_{n_k\cdots(1-n_r)\cdots(1-n_l)\cdots n_1}(t) \\
&+\sum_{l=1}^{k}(1-n_l)\mu_l(t)P_{n_k\cdots(1-n_l)\cdots n_1}(t)
\end{aligned}$$

4.1 Numerical integration of the Kolmogorov equations using 5^{th}-order Runge Kutta

The only practical method for evaluation of the time-dependent state probabilities and functions of these state probabilities, such as moments and cdf's, as well as distributions of absorption times and their moments and cdf's, is via numerical integration of the Kolmogorov forward equations. We could also evaluate these quantities via Monte Carlo sampling methods, but we will not discuss that here.

Next we discuss an alternative model where the state of a territory is *not* a time-dependent binary random variable, rather the time-dependent state of a territory is defined by a random

process representing the *number* of creatures in a specific territory at a particular moment of time. We call this model *The Abundance Model.*

5. The abundance model

Consider a system similar to the occupancy model described above but different in that the population level per territory is now explicitly represented. We assume, for the time being, that any birth/dispersal event consists of the birth/dispersal of exactly one unit (female or mating pair...whatever the unit of analysis happens to be). We also assume, for the time being, that there is no capacity constraint on any of the territories. Both of these (unrealistic) assumptions can be relaxed and add little mathematical complexity to the analysis – they do add some complexity to the coding of the model and therefore will be put off for the present. Definitions given above remain valid with the following changes;

1. $N_i(t) \equiv$ population level in territory i at time t.

2. $\mu_l(t) \equiv$ individual "death" rate for creatures in territory l at time t.

3. $\beta(t) \equiv$ individual "dispersal" rate for creatures at time t.

4. $\alpha_{ij}(t) \equiv$ conditional probability that a particular disperser from territory i goes to territory j, given this disperser disperses from territory i, $i = 1, \cdots, k$, $j = 1, \cdots, k$ at time t. Notice that $\alpha_{ii}(t)$ is the conditional probability that a disperser from territory i stays in territory i — and thus adds to the population level of territory i.

5. $\alpha_{io}(t) \equiv$ conditional probability that a particular disperser goes to territory o (an uninhabitable territory) given this disperser disperses from territory i at time t, $i = 1, \cdots, k$. We define $\alpha_{io}(t) \equiv 1 - \sum_{i=1}^{k} \alpha_{ij}(t)$, and thus $\sum_{i=1}^{k} \alpha_{ij}(t) + \alpha_{io}(t) = 1$.

6. $\theta(t) \equiv$ individual migration rate for creatures at time t.

7. $\gamma_{ij}(t) \equiv$ conditional probability that a creature migrates to territory j given the creature migrates from territory i at time t, $i = 1, \cdots, k$, $j = 1, \cdots, k$, and $\gamma_{ii} \equiv 0$.

8. $\gamma_{io}(t) \equiv$ conditional probability that a creature migrates to territory o (an uninhabitable territory) given the creature migrates from territory i at time t, $i = 1, \cdots, k$.

We consider two cases: the *infinite-capacitaty abundance model* and the *infinite-capacity abundance model.* The former assumes that the territories have unlimited capacity to support creatures and is discussed primarily for pedagogical reasons. The latter is the more realistic case where territories can support a finite number of creatures. Creatures who attempt to enter a territory that is already at its capacity are eliminated.

5.1 The infinite-capacity abundance model

The Kolmogorov forward equations for this species-survival model are:

$$\begin{aligned} P_{n_k \cdots n_1}(t)' &= -\left(\sum_{l=1}^{k} n_l(\mu_l(t) + \theta(t)) + \beta(t) \sum_{l=1}^{k} \sum_{j=1}^{k} n_j \alpha_{jl}(t) \right) P_{n_k \cdots n_1}(t) \\ &+\beta(t) \sum_{l=1}^{k} \sum_{r=1}^{k} \delta_{[n_l]} n_r \alpha_{rl}(t) P_{n_k \cdots n_r \cdots (n_l - 1) \cdots n_1}(t) \\ &+\theta(t) \sum_{l=1}^{k} \sum_{\substack{r=1 \\ r \neq l}}^{k} \delta_{[n_l]} (n_r + 1) \gamma_{rl}(t) P_{n_k \cdots (n_r+1) \cdots (n_l-1) \cdots n_1}(t) \\ &+\theta(t) \sum_{r=1}^{k} (n_r + 1) \gamma_{ro}(t) P_{n_k \cdots (n_r+1) \cdots n_1}(t) \\ &+\sum_{l=1}^{k} (n_l + 1) \mu_l(t) P_{n_k \cdots (n_l+1) \cdots n_1}(t) \end{aligned}$$

for $n_i = 1 \cdots$, and $i = 1 \cdots k$, and

$$\delta_{[a]} = \left\{ \begin{matrix} 1, & a > 0 \\ 0, & a = 0 \end{matrix} \right\}.$$

The clever reader will immediately notice that this model can be viewed as a *queueing network* model – but of course most real-world systems and models of those systems can be viewed as a special case of a queueing network model.

$$
\begin{aligned}
\frac{d}{dt}\mathrm{E}\left[N_j(t)\right] &= \sum_{n_k=0}^{\infty}\cdots\sum_{n_j=0}^{\infty}\cdots\sum_{n_1=0}^{\infty} n_j\cdot\Pr(N_j(t)=n_j)' \\
&= \sum_{n_k=0}^{\infty}\cdots\sum_{n_j=0}^{\infty}\cdots\sum_{n_1=0}^{\infty} n_j\cdot\left\{-\left(\sum_{l=1}^{k} n_l(\mu_l(t)+\theta(t))+\beta(t)\sum_{l=1}^{k}\sum_{r=1}^{k} n_r\alpha_{rl}(t)\right)\ P_{n_k\cdots n_1}(t)\right. \\
&\quad +\beta(t)\sum_{l=1}^{k}\sum_{r=1}^{k}\delta_{[n_l]}n_r\alpha_{rl}(t)P_{n_k\cdots n_r\cdots(n_l-1)\cdots n_1}(t) \\
&\quad +\theta(t)\sum_{l=1}^{k}\sum_{\substack{r=1\\ r\neq l}}^{k}\delta_{[n_l]}(n_r+1)\gamma_{rl}(t)P_{n_k\cdots(n_r+1)\cdots(n_l-1)\cdots n_1}(t) \\
&\quad +\theta(t)\sum_{r=1}^{k}(n_r+1)\gamma_{ro}(t)P_{n_k\cdots(n_r+1)\cdots n_1}(t) \\
&\quad \left.+\sum_{l=1}^{k}(n_l+1)\mu_l(t)P_{n_k\cdots(n_l+1)\cdots n_1}(t)\right\} \\
&= -\sum_{l=1}^{k}\mu_l(t)\mathrm{E}\left[N_l(t)N_j(t)\right]-\theta(t)\sum_{l=1}^{k}\mathrm{E}\left[N_l(t)N_j(t)\right] \\
&\quad -\beta(t)\sum_{l=1}^{k}\sum_{r=1}^{k}\alpha_{rl}(t)\mathrm{E}\left[N_r(t)N_j(t)\right] \\
&\quad +\beta(t)\sum_{l=1}^{k}\sum_{r=1}^{k}\alpha_{rl}(t)\mathrm{E}\left[N_r(t)N_j(t)\right]+\beta(t)\sum_{r=1}^{k}\alpha_{rj}(t)\mathrm{E}\left[N_r(t)\right] \\
&\quad +\theta(t)\sum_{l=1}^{k}\sum_{\substack{r=1\\ r\neq l}}\gamma_{rl}(t)\mathrm{E}\left[N_j(t)N_r(t)\right] \\
&\quad -\theta(t)\left(\sum_{\substack{l=1\\ l\neq j}}^{k}\gamma_{jl}(t)\mathrm{E}\left[N_j(t)\right]-\sum_{\substack{r=1\\ r\neq j}}^{k}\gamma_{rj}(t)\mathrm{E}\left[N_r(t)\right]\right)
\end{aligned}
$$

$$
\begin{aligned}
&+\theta(t)\left(\sum_{r=1}^{k}\gamma_{ro}(t)\mathrm{E}\left[N_j(t)N_r(t)\right]-\gamma_{jo}(t)\mathrm{E}\left[N_j(t)\right]\right)\\
&+\sum_{l=1}^{k}\mu_l(t)\mathrm{E}\left[N_j(t)N_l(t)\right]-\mu_j(t)\mathrm{E}\left[N_j(t)\right]\\
=\;&\beta(t)\sum_{r=1}^{k}\alpha_{rj}(t)\mathrm{E}\left[N_r(t)\right]\\
&-\theta(t)\left(\sum_{\substack{l=1\\l\neq j}}^{k}\gamma_{jl}(t)\mathrm{E}\left[N_j(t)\right]-\sum_{\substack{r=1\\r\neq j}}^{k}\gamma_{rj}(t)\mathrm{E}\left[N_r(t)\right]\right)\\
&-\theta(t)\gamma_{jo}(t)\mathrm{E}\left[N_j(t)\right]\\
&-\mu_j(t)\mathrm{E}\left[N_j(t)\right]
\end{aligned}
$$

and so

$$
\begin{aligned}
\frac{d}{dt}\mathrm{E}\left[N_j(t)\right]=\theta(t)\sum_{r=1}^{k}\gamma_{rj}(t)\mathrm{E}\left[N_r(t)\right]+\beta(t)\sum_{r=1}^{k}\alpha_{rj}(t)\mathrm{E}\left[N_r(t)\right]\\
-\mu_j(t)\mathrm{E}\left[N_j(t)\right]-\theta(t)\mathrm{E}\left[N_j(t)\right]
\end{aligned}
$$

5.1.1 Direct evaluation of model performance measures via numerical integration

5.1.2 State-space explosions and the combinatorics of abundance models

5.1.3 Approximations for time-dependent occupancy and abundance models

5.1.4 The simple *independence*-type approximation

5.1.5 Approximation definitions and a numerical evaluation method

5.1.6 Where the approximations works well

5.1.7 Where the approximation works no better than the flying ability of small dogs

5.1.8 Example: the infinite-capacity abundance model and its evaluation

Consider a system consisting of 5 territories and a collection of green-eared, floppy jackalopes.

5.2 The finite-capacity abundance model

In this section we consider the case where one or more of the territories has capacity to support only a finite number of creatures. Creatures attempting to migrage into a territory that is already at it's capacity are unsuccessful and die. Creatures that born to current residents of the territories and choose to stay in their birth-territory cannot survive if their territory is already at capacity.

Notice that a special case of this model is the occupancy model from the first section (setting the capacity to 1.)

5.2.1 The Kolmogorov forward equations

The Kolmogorov forward equations for this species-survival model are:

$$\begin{aligned}
P_{n_k\cdots n_1}(t)' &= -\left(\sum_{l=1}^{k} n_l(\mu_l(t)+\theta_l(t)) + \beta(t)\sum_{l=1}^{k}\sum_{j=1}^{k} n_j\alpha_{j,l}(t)\right) P_{n_k\cdots n_1}(t) \\
&+\beta(t)\sum_{l=1}^{k}\sum_{r=1}^{k}\delta_{[n_l]}n_r\alpha_{rl}(t)P_{n_k\cdots n_r\cdots(n_l-1)\cdots n_1}(t) \\
&+\sum_{l=1}^{k}\sum_{\substack{r=1\\ r\neq l}}^{k}\delta_{[n_l]}\delta_{[c_r-n_r]}\theta_r(t)(n_r+1)\gamma_{rl}(t)P_{n_k\cdots(n_r+1)\cdots(n_l-1)\cdots n_1}(t) \\
&\sum_{r=1}^{k}\delta_{[c_r-n_r]} + \theta_r(t)(n_r+1)\gamma_{ro}(t)P_{n_k\cdots(n_r+1)\cdots n_1}(t) \\
&+\sum_{l=1}^{k}\delta_{[c_l-n_l]}(n_l+1)\mu_l(t)P_{n_k\cdots(n_l+1)\cdots n_1}(t)
\end{aligned}$$

for $n_i = 1\cdots c_i$, and $i = 1\cdots k$. The clever reader will immediately notice that this model can be viewed as a *queueing network* model – but of course most real-world systems and models of those systems can be viewed as a special case of a queueing network model.

********** The following has not been entered yet -

but is *almost* the same as:

$$
\begin{aligned}
\frac{d}{dt}\mathrm{E}\left[N_j(t)\right] &= \sum_{n_k=0}^{\infty}\cdots\sum_{n_j=0}^{\infty}\cdots\sum_{n_1=0}^{\infty} n_j\cdot\Pr(N_j(t)=n_j)' \\
&= \sum_{n_k=0}^{\infty}\cdots\sum_{n_j=0}^{\infty}\cdots\sum_{n_1=0}^{\infty} n_j\cdot\Bigg\{-\left(\sum_{l=1}^{k} n_l(\mu_l(t)+\theta_l(t))+\beta(t)\sum_{l=1}^{k}\sum_{r=1}^{k} n_r\alpha_{rl}(t)\right) P_{n_k\cdots n_1}(t) \\
&\quad +\beta(t)\sum_{l=1}^{k}\sum_{r=1}^{k}\delta_{[n_l]}n_r\alpha_{rl}(t)P_{n_k\cdots n_r\cdots(n_l-1)\cdots n_1}(t) \\
&\quad +\sum_{l=1}^{k}\sum_{\substack{r=1\\ r\neq l}}^{k}\delta_{[n_l]}\delta[c_r-n_r](n_r+1)\theta_r(t)\gamma_{rl}(t)P_{n_k\cdots(n_r+1)\cdots(n_l-1)\cdots n_1}(t) \\
&\quad +\sum_{r=1}^{k}\delta[c_r-n_r](n_r+1)\theta_r(t)\gamma_{ro}(t)P_{n_k\cdots(n_r+1)\cdots n_1}(t) \\
&\quad +\sum_{l=1}^{k}\delta[c_l-n_l](n_l+1)\mu_l(t)P_{n_k\cdots(n_l+1)\cdots n_1}(t)\Bigg\} \\
&= -\sum_{l=1}^{k}\mu_l(t)\mathrm{E}\left[N_l(t)N_j(t)\right]-\sum_{l=1}^{k}\theta_l(t)\mathrm{E}\left[N_l(t)N_j(t)\right] \\
&\quad -\beta(t)\sum_{l=1}^{k}\sum_{r=1}^{k}\alpha_{rl}(t)\mathrm{E}\left[N_r(t)N_j(t)\right] \\
&\quad +\beta(t)\sum_{l=1}^{k}\sum_{r=1}^{k}\alpha_{rl}(t)\mathrm{E}\left[N_r(t)N_j(t)\right]+\beta(t)\sum_{r=1}^{k}\alpha_{rj}(t)\mathrm{E}\left[N_r(t)\right] \\
&\quad +\sum_{l=1}^{k}\sum_{\substack{r=1\\ r\neq l}}\theta_r(t)\gamma_{rl}(t)\mathrm{E}\left[N_j(t)N_r(t)\right] \\
&\quad -\left(\sum_{\substack{l=1\\ l\neq j}}^{k}\theta_j(t)\gamma_{jl}(t)\mathrm{E}\left[N_j(t)\right]-\sum_{\substack{r=1\\ r\neq j}}^{k}\theta_r(t)\gamma_{rj}(t)\mathrm{E}\left[N_r(t)\right]\right) \\
&\quad +\left(\sum_{r=1}^{k}\theta_r(t)\gamma_{ro}(t)\mathrm{E}\left[N_j(t)N_r(t)\right]-\theta_j(t)\gamma_{jo}(t)\mathrm{E}\left[N_j(t)\right]\right) \\
&\quad +\sum_{l=1}^{k}\mu_l(t)\mathrm{E}\left[N_j(t)N_l(t)\right]-\mu_j(t)\mathrm{E}\left[N_j(t)\right]
\end{aligned}
$$

$$
\begin{aligned}
&= \beta(t)\sum_{r=1}^{k}\alpha_{rj}(t)\mathrm{E}\left[N_r(t)\right] \\
&\quad -\left(\sum_{\substack{l=1\\ l\neq j}}^{k}\theta_j(t)\gamma_{jl}(t)\mathrm{E}\left[N_j(t)\right]-\sum_{\substack{r=1\\ r\neq j}}^{k}\theta_r(t)\gamma_{rj}(t)\mathrm{E}\left[N_r(t)\right]\right) \\
&\quad -\theta_j(t)\gamma_{jo}(t)\mathrm{E}\left[N_j(t)\right] \\
&\quad -\mu_j(t)\mathrm{E}\left[N_j(t)\right] \\
&= \beta(t)\sum_{r=1}^{k}\alpha_{rj}(t)\mathrm{E}\left[N_r(t)\right] \\
&\quad +\sum_{\substack{r=1\\ r\neq j}}^{k}\theta(t)_r\gamma_{rj}(t)\mathrm{E}\left[N_r(t)\right] \\
&\quad -\theta_j(t)\mathrm{E}\left[N_j(t)\right] \\
&\quad -\mu_j(t)\mathrm{E}\left[N_j(t)\right]
\end{aligned}
$$

which reduces to

$$
\begin{aligned}
\frac{d}{dt}\mathrm{E}\left[N_j(t)\right] = \quad & \sum_{r=1}^{k}\theta_r(t)\gamma_{rj}(t)\mathrm{E}\left[N_r(t)|N_j(t)\neq c_j\right]\mathrm{P}\left(N_j(t)\neq c_j\right) \\
& +\beta(t)\sum_{r=1}^{k}\alpha_{rj}(t)\left[N_r(t)|N_j(t)\neq c_j\right]\mathrm{P}\left(N_j(t)\neq c_j\right) \\
& -\left(\mu_j(t)+\theta_j(t)\right)\mathrm{E}\left[N_j(t)\right]
\end{aligned}
$$

5.2.2 A closure approximation for the moment differential equations

In this section we describe an approximation that will *close* the set of moment differential equations listed above. Our closure approximation consists of two steps and is analogous to excellent approximations made in queueuing theory (see Taaffe 1984, ..., 2002).

The closure approximation consists of two components. The first compoment is:

$$
\mathrm{E}\left[N_r(t)|N_j(t)<c_j\right]\mathrm{P}\left(N_j(t)<c_j\right)\approx\mathrm{E}\left[N_r(t)\right]\mathrm{P}\left(N_j(t)<c_j\right)
$$

The second approximation is the use of a *surrogate* distribution to approximate

$$\mathrm{P}\left(N_j(t) < c_j\right) \approx \mathrm{P}\left(X < n\right)$$

where $X \sim \texttt{binomial}(n, p)$ for $n = c_j$, and $p = \mathrm{E}\left[N_j(t)\right]/c_j$.

This works well .... blah, blah, blah... I can write this pretty quickly (for your understanding etc.)... But it is time to go to the dentist and then meetings and then teaching...

5.2.3 Where the approximations works well

5.2.4 Where the approximation works no better than the flying ability of small dogs

5.2.5 Example: the finite-capacity abundance model and its evaluation

6. Conclusions

7. Acknowledgments

8. References

9. Appendix A: Maple 7 code

10. Appendix B: Proofs and derivations

Appendix 3

Spatially Explicit Markov Models for Designing Habitat Reserves

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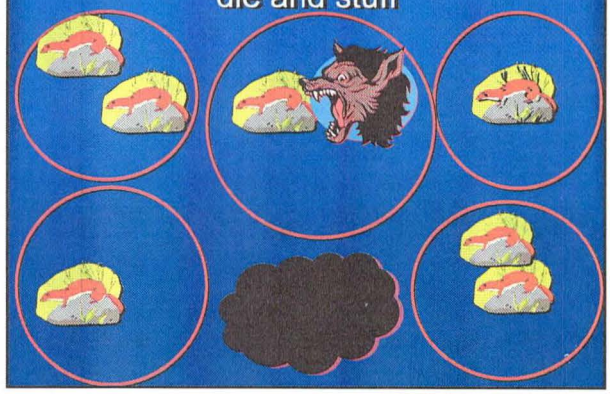
Punta de Tralca, Chile
March 4 - 7, 2002

1

Ferrets are born and migrate and die and stuff



The Deterministic Differential Equation (DDE) Abundance Model

$$X_j(t)' \equiv \frac{d}{dt} X_j(t) = \beta(t) \sum_{r=1}^{k} \alpha_{rj}(t) X_r(t)$$

$$+ \sum_{r=1}^{k} \theta_r(t) \gamma_{rj}(t) X_r(t)$$

$$- \theta_j(t) X_j(t) - \mu_j(t) X_j(t)$$

3

DDE Model

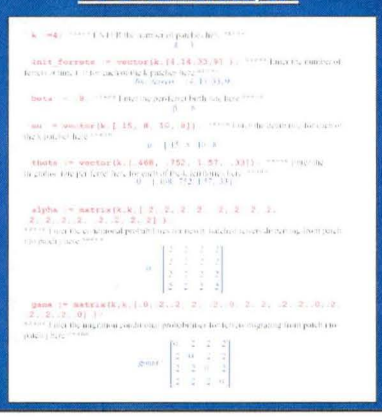
The MAPLE code (.mws)

The MAPLE code (.pdf)

4

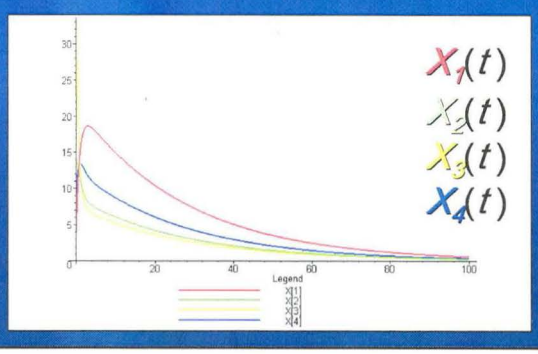
DDE: *Example*

INPUT



5

The Number of Ferrets in Territory i at time t

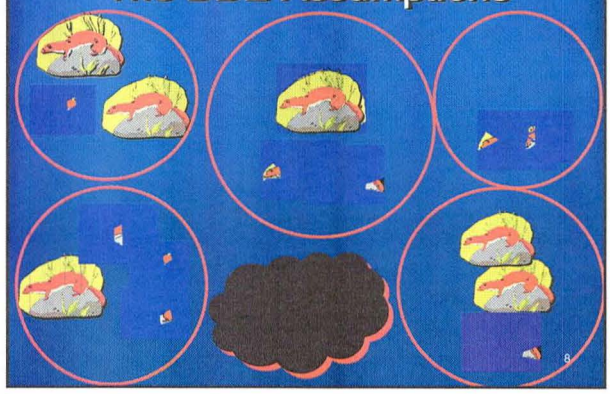


Limitations of The DDE Model

- Ferrets tend *not* to be *infinitely divisible* – at least not cheerfully.
- *Models are not* (humanely) *interpretable for small-populations.*

7

The DDE Assumptions



8

The Stochastic Abundance Model - Infinite Capacity: *Input*

$N_i(t) \equiv$ population level in territory i at time t, for $i = 1, \cdots, k$

$\mu_i(t) \equiv$ individual death rate for creatures in territory I at time t, for $i = 1, \cdots, k$

$\beta(t) \equiv$ individual dispersal (birth) rate for creatures at time t

$\alpha_{ij}(t) \equiv$ conditional probability that a particular disperser from territory i goes to territory j, given this disperser disperses from territory i, at time t, for $i = 1, \cdots, k$, $j = 1, \cdots, k$, at time t.

$\alpha_{io}(t) \equiv$ conditional probability that a particular disperser from territory i goes to territory o (an uninhabitable territory), given this disperser disperses from territory i, at time t, for $i = 1, \cdots, k$.

$\theta_i(t) \equiv$ individual migration rate for creatures in territory i at time t, for $i = 1, \cdots, k$.

$\gamma_{ij}(t) \equiv$ conditional probability that a particular migrating creature from territory i migrates to territory j, at time t, for $i = 1, \cdots, k$, $j = 1, \cdots k$, and $\gamma_{ii}(t) \equiv 0$, at time t.

$\gamma_{io}(t) \equiv$ conditional probability that a particular migrating creature from territory i migrates to territory o (an uninhabitable territory), at time t, for $i = 1, \cdots, k$.

9

The Stochastic Abundance Model - Infinite Capacity: *Output*

$$P_{n_k n_{k-1} \cdots n_1}(t) \equiv \mathrm{P}\left(N_k(t) = n_k, N_{k-1}(t) = n_{k-1}, \cdots, N_1(t) = n_1\right)$$

$$\mathrm{E}[\mathbf{N}(t)] \equiv \left(\mathrm{E}[N_k(t)], \mathrm{E}[N_k(t)], \cdots, \mathrm{E}[N_1(t)]\right)$$

$$\mathrm{Var}[\mathbf{N}(t)] \equiv \left(\mathrm{Var}[N_k(t)], \mathrm{Var}[N_k(t)], \cdots, \mathrm{Var}[N_1(t)]\right)$$

$$\mathrm{E}\left[\sum_{i=1}^{k} N_i(t)\right] \text{ and } \mathrm{Var}\left[\sum_{i=1}^{k} N_i(t)\right]$$

$P(N_i(t) = 0) \equiv P(\text{Extinction exists in territory } i \text{ at time } t)$

10

The Kolmogorov forward equations

$$P_{n_k \cdots n_1}(t)' \equiv -\left(\sum_{l=1}^{k} n_l\left(\mu_l(t) + \theta_l(t)\right) + \beta(t)\sum_{l=1}^{k}\sum_{j=1}^{k} n_j \alpha_{jl}(t)\right) P_{n_k \cdots n_1}(t)$$

$$+\beta(t)\sum_{l=1}^{k}\sum_{r=1}^{k} \delta_{[n_l]} n_r \alpha_{rl}(t)\, P_{n_k \cdots n_r \cdots (n_l - 1) \cdots n_1}(t)$$

$$+\sum_{l=1}^{k}\sum_{\substack{r=1 \\ r \neq l}}^{k} \delta_{[n_l]}\left(n_r + 1\right)\theta_r(t)\gamma_{rl}(t) P_{n_k \cdots (n_r+1) \cdots (n_l - 1) \cdots n_1}(t)$$

$$+\sum_{r=1}^{k}\left(n_r + 1\right)\theta_r(t)\gamma_{ro}(t) P_{n_k \cdots (n_r+1) \cdots n_1}(t)$$

$$+\sum_{l=1}^{k}\left(n_l + 1\right)\mu_l(t)\, P_{n_k \cdots (n_l+1) \cdots n_1}(t)$$

for $n_i = 1, \cdots, \infty$, and $i = 1, \cdots, k$, and $\delta_{[a]} = \begin{cases} 1, & a > 0 \\ 0, & a = 0 \end{cases}$

11

The Kolmogorov forward equations

$$P_{n_k \cdots n_1}(t)' \equiv -\left(\sum_{l=1}^{k} n_l\left(\mu_l(t) + \theta_l(t)\right) + \beta(t)\sum_{l=1}^{k}\sum_{j=1}^{k} n_j \alpha_{jl}(t)\right) P_{n_k \cdots n_1}(t)$$

$$+\beta(t)\sum_{l=1}^{k}\sum_{r=1}^{k} \delta_{[n_l]} n_r \alpha_{rl}(t)\, P_{n_k \cdots n_r \cdots (n_l - 1) \cdots n_1}(t)$$

$$+\sum_{l=1}^{k}\sum_{\substack{r=1 \\ r \neq l}}^{k} \delta_{[n_l]}\left(n_r + 1\right)\theta_r(t)\gamma_{rl}(t) P_{n_k \cdots (n_r+1) \cdots (n_l - 1) \cdots n_1}(t)$$

$$+\sum_{r=1}^{k}\left(n_r + 1\right)\theta_r(t)\gamma_{ro}(t) P_{n_k \cdots (n_r+1) \cdots n_1}(t)$$

$$+\sum_{l=1}^{k}\left(n_l + 1\right)\mu_l(t)\, P_{n_k \cdots (n_l+1) \cdots n_1}(t)$$

for $n_i = 1, \cdots, \infty$, and $i = 1, \cdots, k$, and $\delta_{[a]} = \begin{cases} 1, & a > 0 \\ 0, & a = 0 \end{cases}$

12

Moment Diff 'l Equations (MDE's)

$$\mathrm{E}\left[N_j(t)\right]' \equiv \frac{d}{dt}\mathrm{E}\left[N_j(t)\right] = \sum_{i=0}^{\infty} i \cdot \mathrm{P}(N_j(t)=i)' = \sum_{n_k=0}^{\infty}\sum_{n_{k-1}=0}^{\infty}\cdots\sum_{n_j=0}^{\infty}\cdots\sum_{n_2=0}^{\infty}\sum_{n_1=0}^{\infty} n_j \cdot P_{n_k,\cdots,n_1}(t)'$$

$$= \sum_{n_k=0}^{\infty}\cdots\sum_{n_j=0}^{\infty}\cdots\sum_{n_1=0}^{\infty} n_j \left[-\left(\sum_{l=1}^{k} n_l \left(\mu_l(t)+\theta_l(t)\right) + \beta(t)\sum_{l=1}^{k}\sum_{j=1}^{k} n_l \alpha_{jl}(t) \right) P_{n_k,\cdots,n_1}(t) \right.$$

$$+\beta(t)\sum_{l=1}^{k}\sum_{r=1}^{k}\delta_{[n_j]} n_r \alpha_{jl}(t)\, P_{n_k,\cdots,n_r-(n_j-1),\cdots,n_1}(t)$$

$$+\sum_{l=1}^{k}\sum_{\substack{r=1\\ r\neq l}}^{k}\delta_{[n_j]}\left(n_r+1\right)\theta_r(t)\gamma_{rl}(t) P_{n_k,\cdots,(n_r+1),\cdots,(n_l-1),\cdots,n_1}(t)$$

$$\left. +\sum_{r=1}^{k}\left(n_r+1\right)\theta_r(t)\gamma_{rj}(t) P_{n_k,\cdots,(n_r+1),\cdots,n_1}(t) + \sum_{l=1}^{k}\left(n_l+1\right)\mu_l(t)\, P_{n_k,\cdots,(n_l+1),\cdots,n_1}(t) \right]$$

13

MDE 's

$$\mathrm{E}\left[N_j(t)\right]' = \beta(t)\sum_{r=1}^{k}\alpha_{rj}(t)\,\mathrm{E}\left[N_r(t)\right]$$

$$+\sum_{r=1}^{k}\theta_r(t)\gamma_{rj}(t)\mathrm{E}\left[N_r(t)\right]$$

$$-\theta_j(t)\mathrm{E}\left[N_j(t)\right] - \mu_j(t)\mathrm{E}\left[N_j(t)\right]$$

Closed set of MDE's!

15

MDE 's

$$\mathrm{E}\left[N_j(t)\right]' = \beta(t)\sum_{r=1}^{k}\alpha_{rj}(t)\,\mathrm{E}\left[N_r(t)\right]$$

$$+\sum_{r=1}^{k}\theta_r(t)\gamma_{rj}(t)\mathrm{E}\left[N_r(t)\right]$$

$$-\theta_j(t)\mathrm{E}\left[N_j(t)\right] - \mu_j(t)\mathrm{E}\left[N_j(t)\right]$$

14

MDE's vs. DDE's: small populations

$$\mathrm{E}\left[N_j(t)\right]' = \beta(t)\sum_{r=1}^{k}\alpha_{rj}(t)\,\mathrm{E}\left[N_r(t)\right]$$

$$\mathrm{E}\left[N_j(0)\right] + \int_0^t \mathrm{E}\left[N_j(\tau)\right]' d\tau \qquad +\sum_{r=1}^{k}\theta_r(t)\gamma_{rj}(t)\mathrm{E}\left[N_r(t)\right]$$

Interpretable

$$-\theta_j(t)\mathrm{E}\left[N_j(t)\right] - \mu_j(t)\mathrm{E}\left[N_j(t)\right]$$

$$X_j(t)' = \beta(t)\sum_{r=1}^{k}\alpha_{rj}(t)\,X_r(t)$$

$$X_j(0) + \int_0^t X_j'(\tau)\,d\tau \qquad +\sum_{r=1}^{k}\theta_r(t)\gamma_{rj}(t)\,X_r(t)$$

Not interpretable

$$-\theta_j(t)X_j(t) - \mu_j(t)\,X_j(t)$$

17

The Stochastic Abundance Model - Infinite Capacity:

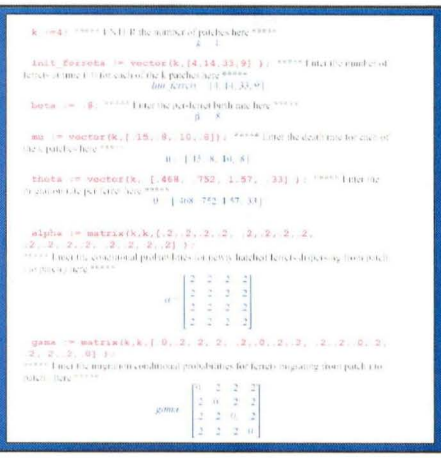
Example (*same as the DDE*)

MAPLE 7 Code (.mws file)

MAPLE 7 Code (.pdf file)

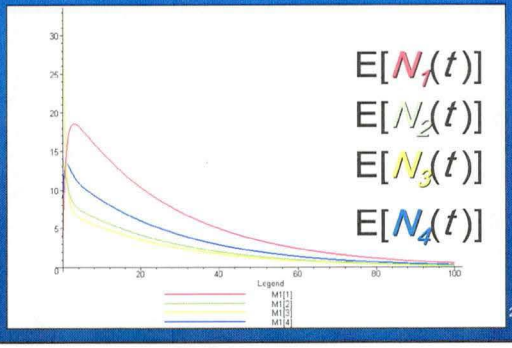
21

INPUT



22

The Expected Number of Ferrets in Territory i at time t



$E[N_1(t)]$

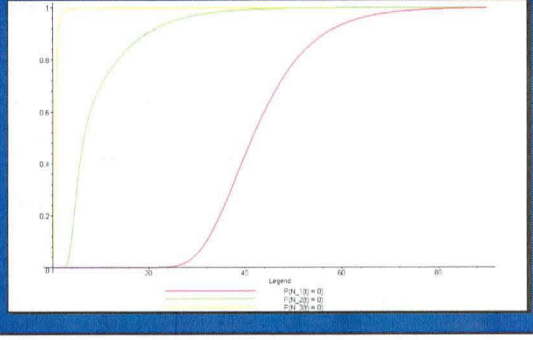
$E[N_2(t)]$

$E[N_3(t)]$

$E[N_4(t)]$

Extinction Probability Function

$P(N_j(t)=0)$ vs. t



Extinction Probability Function

$P(N_j(t)=0)$ vs. t

Assume that $N_j(t)$ is approximately $\sim$ Poisson$\left(\mathrm{E}\left[N_j(t)\right]\right)$

So $P(N_j(t)=0) \approx \dfrac{\left(\mathrm{E}\left[N_j(t)\right]\right)^0 \exp\left(-\mathrm{E}\left[N_j(t)\right]\right)}{\left(\mathrm{E}\left[N_j(t)\right]\right)!}$

$\therefore P(N_j(t)=0) \approx \exp\left(-\mathrm{E}\left[N_j(t)\right]\right)$

Not available in the DDE Model

The Stochastic Abundance Model - Finite-Capacity: *Input*

The same input as the infinite capacity model and

$c_i \equiv$ capacity of territory i

The Stochastic Abundance Model - Finite-Capacity: *Output*

$$P_{n_k n_{k-1} \cdots n_1}(t) \equiv \mathrm{P}\left(N_k(t)=n_k, N_{k-1}(t)=n_{k-1}, \cdots, N_1(t)=n_1\right)$$

$$\mathrm{E}[\mathbf{N}(t)] \equiv \left(\mathrm{E}[N_k(t)], \mathrm{E}[N_k(t)], \cdots, \mathrm{E}[N_1(t)]\right)$$

$$\mathrm{Var}[\mathbf{N}(t)] \equiv \left(\mathrm{Var}[N_k(t)], \mathrm{Var}[N_k(t)], \cdots, \mathrm{Var}[N_1(t)]\right)$$

$$\mathrm{E}\left[\sum_{i=1}^{k} N_i(t)\right] \text{ and } \mathrm{Var}\left[\sum_{i=1}^{k} N_i(t)\right]$$

$P(N_i(t)=0) \equiv P(\text{Extinction exists in territory } i \text{ at time } t)$

The Kolmogorov forward equations

$$P_{n_k \cdots n_1}(t)' \equiv -\left(\sum_{l=1}^{k} n_l\left(\mu_l(t)+\theta_l(t)\right)+\beta(t)\sum_{l=1}^{k}\sum_{j=1}^{k} n_j \alpha_{jl}(t)\right) P_{n_k \cdots n_1}(t)$$

$$+\beta(t)\sum_{l=1}^{k}\sum_{r=1}^{k} \delta_{[n_l]} n_r \alpha_{rl}(t)\, P_{n_k \cdots n_r \cdots (n_l-1) \cdots n_1}(t)$$

$$+\sum_{l=1}^{k}\sum_{\substack{r=1 \\ r\neq l}}^{k} \delta_{[n_l]}\delta_{[c_r-n_r]}\left(n_r+1\right)\theta_r(t)\gamma_{rl}(t) P_{n_k \cdots (n_r+1) \cdots (n_l-1) \cdots n_1}(t)$$

$$+\sum_{r=1}^{k} \delta_{[c_r-n_r]}\left(n_r+1\right)\theta_r(t)\gamma_{ro}(t) P_{n_k \cdots (n_r+1) \cdots n_1}(t)$$

$$+\sum_{l=1}^{k} \delta_{[c_l-n_l]}\left(n_l+1\right)\mu_l(t)\, P_{n_k \cdots (n_l+1) \cdots n_1}(t)$$

for $n_i = 1, \cdots \boxed{c_i}$, and $i = 1, \cdots, k$, and $\delta_{[a]} = \begin{cases} 1, & a > 0 \\ 0, & a = 0 \end{cases}$

The Kolmogorov forward equations

The number of states, and thus the number of Kolmogorov forward Equations is

$$M \equiv \prod_{j=1}^{k} c_j .$$

So for a four-territory model where each territory has a carrying capacity of one hundred,

$M = 100,000,000.$

Approximations needed for large-population, many-territory stochastic models!

K Moment Diff 'l Equations (*MDE*'s)

$$\mathrm{E}\left[N_j(t)\right]' = \sum_{n_j=0}^{c_j} i \cdot \mathrm{P}(N_j(t)=i)' = \sum_{n_k=0}^{c_k}\sum_{n_{k-1}=0}^{c_{k-1}}\cdots\sum_{n_j=0}^{c_j}\cdots\sum_{n_2=0}^{c_2}\sum_{n_1=0}^{c_1} n_j \cdot P_{n_k,\cdots,n_1}(t)'$$

$$= \sum_{n_k=0}^{c_k}\cdots\sum_{n_j=0}^{c_j}\cdots\sum_{n_1=0}^{c_1} n_j \left[-\left(\sum_{i=1}^{k} n_i\left(\mu_i(t)+\theta_i(t)\right)+\beta(t)\sum_{i=1}^{k}\sum_{j=1}^{k} n_i\alpha_{ij}(t)\right) P_{n_k,\cdots,n_1}(t) \right.$$

$$+\beta(t)\sum_{i=1}^{k}\sum_{r=1}^{k}\delta_{[n_j]} n_i \alpha_{ri}(t)\, P_{n_k,\cdots,n_r-(n_j-1),\cdots,n_1}(t)$$

$$+\sum_{i=1}^{k}\sum_{r=1}^{k}\delta_{[n_j]}\delta_{[c_r-n_r]}\left(n_r+1\right)\theta_r(t)\gamma_{ri}(t) P_{n_k,\cdots,(n_r+1),\cdots,(n_i-1),\cdots,n_1}(t)$$

$$+\sum_{r=1}^{k}\delta_{[c_r-n_r]}\left(n_r+1\right)\theta_r(t)\gamma_{rr}(t) P_{n_k,\cdots,(n_r+1),\cdots,n_1}(t)$$

$$\left.+\sum_{i=1}^{k}\delta_{[c_j-n_j]}\left(n_i+1\right)\mu_i(t)\, P_{n_k,\cdots,(n_j+1),\cdots,n_1}(t)\right]$$

32

K Moment Diff 'l Equations (*MDE*'s)

$$\mathrm{E}\left[N_j(t)\right]' = \beta(t)\sum_{r=1}^{k}\alpha_{rj}(t)\,\mathrm{E}\left[N_r(t)\,|\,N_j(t)<c_j\right]P\left(N_j(t)<c_j\right)$$

$$+\sum_{r=1}^{k}\theta_r(t)\gamma_{rj}(t)\mathrm{E}\left[N_r(t)\,|\,N_j(t)<c_j\right]P\left(N_j(t)<c_j\right)$$

$$-\theta_j(t)\mathrm{E}\left[N_j(t)\right]-\mu_j(t)\mathrm{E}\left[N_j(t)\right]$$

Not Closed !

33

Closure Approximation

1) Let $\mathrm{E}\left[N_r(t), N_j(t)<c_j\right] \approx \mathrm{E}\left[N_r(t)\right]P\left(N_j(t)<c_j\right)$

where $\mathrm{E}\left[N_r(t), N_j(t)<c_j\right] \equiv \sum_{n_r=0}^{c_r} n_r P\left(N_r(t)=n_r, N_j(t)<c_j\right)$

(and is called a "partial moment"), for $r = 1,\cdots,k$, and $j = 1,\cdots,k$.

2) Let $P(N_j(t)=c_j) \approx P(X=c_j)$

where $X \sim$ binomial$\left(c_j, \mathrm{E}\left[N_j(t)\right]/c_j\right)$

so $P(N_j(t)=c_j) \approx \binom{c_j}{c_j}\left(\mathrm{E}\left[N_j(t)\right]/c_j\right)^{c_j}\left(1-\mathrm{E}\left[N_j(t)\right]/c_j\right)^{c_j-c_j}$

$\therefore$ $P(N_j(t)=c_j) \approx \left(\mathrm{E}\left[N_j(t)\right]/c_j\right)^{c_j}$

34

K MDE 's

$$\mathrm{E}\left[N_j(t)\right]' \approx \beta(t)\sum_{r=1}^{k}\alpha_{rj}(t)\,\mathrm{E}\left[N_r(t)\right]P\left(N_j(t)<c_j\right)$$

$$+\sum_{r=1}^{k}\theta_r(t)\gamma_{rj}(t)\mathrm{E}\left[N_r(t)\right]P\left(N_j(t)<c_j\right)$$

$$-\theta_j(t)\mathrm{E}\left[N_j(t)\right]-\mu_j(t)\mathrm{E}\left[N_j(t)\right]$$

so $\mathrm{E}\left[N_j(t)\right]' \approx \beta(t)\sum_{r=1}^{k}\alpha_{rj}(t)\,\mathrm{E}\left[N_r(t)\right]\left(1-\left(\mathrm{E}\left[N_j(t)\right]/c_j\right)^{c_j}\right)$

$$+\sum_{r=1}^{k}\theta_r(t)\gamma_{rj}(t)\mathrm{E}\left[N_r(t)\right]\left(1-\left(\mathrm{E}\left[N_j(t)\right]/c_j\right)^{c_j}\right)$$

$$-\theta_j(t)\mathrm{E}\left[N_j(t)\right]-\mu_j(t)\mathrm{E}\left[N_j(t)\right]$$

35

K MDE 's

$$\frac{d}{dt}\mathrm{E}\left[N_j(t)\right] \approx \beta(t)\sum_{r=1}^{k}\alpha_{rj}(t)\,\mathrm{E}\left[N_r(t)\right]\left(1-\left(\mathrm{E}\left[N_j(t)\right]/c_j\right)^{c_j}\right)$$

$$+\sum_{r=1}^{k}\theta_r(t)\gamma_{rj}(t)\mathrm{E}\left[N_r(t)\right]\left(1-\left(\mathrm{E}\left[N_j(t)\right]/c_j\right)^{c_j}\right)$$

$$-\theta_j(t)\mathrm{E}\left[N_j(t)\right]-\mu_j(t)\mathrm{E}\left[N_j(t)\right]$$

Pseudo-Closed!

36

The Stochastic Abundance Model - Finite Capacity: Examples

MAPLE 7 Code (.mws file)

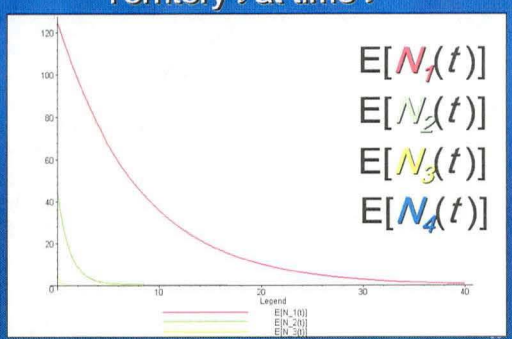
MAPLE 7 Code (.pdf file)

37

INPUT

38

The Expected Number of Ferrets in Territory i at time t



$E[N_1(t)]$

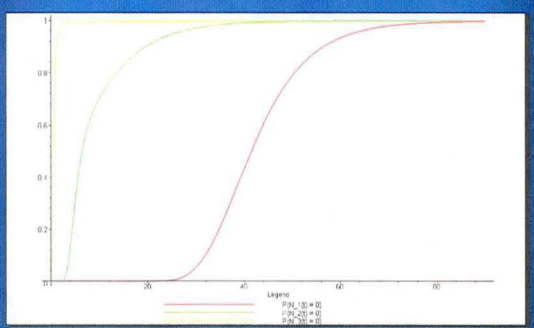
$E[N_2(t)]$

$E[N_3(t)]$

$E[N_4(t)]$

Extinction Probability function

$P\left(N_j(t)=0\right)$ vs. t

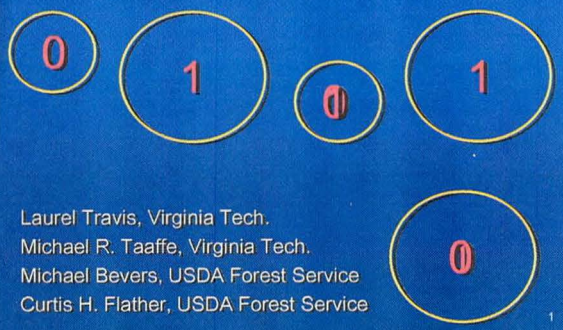


Thank you for your attention!

42

Appendix 4

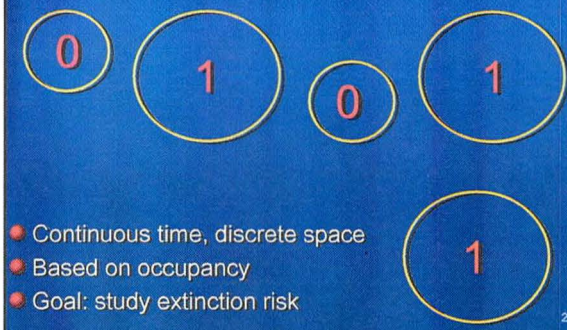
Markov models of endangered species populations and habitat



Laurel Travis, Virginia Tech.
Michael R. Taaffe, Virginia Tech.
Michael Bevers, USDA Forest Service
Curtis H. Flather, USDA Forest Service

1

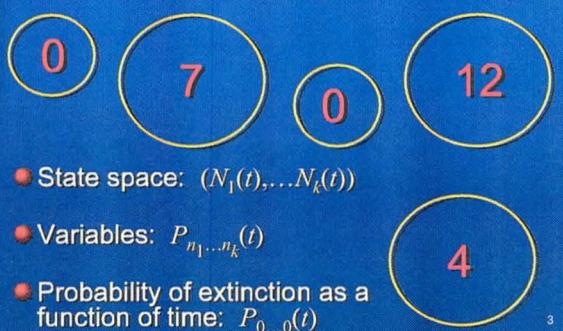
Metapopulation approach



- Continuous time, discrete space
- Based on occupancy
- Goal: study extinction risk

2

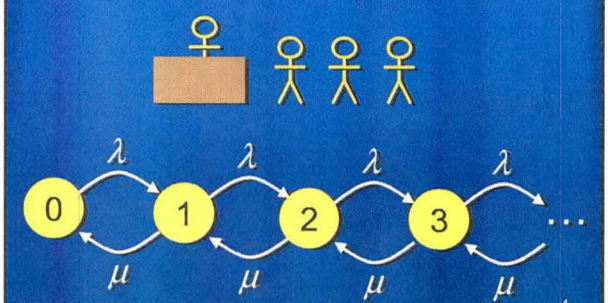
Does abundance matter?



- State space: $(N_1(t),\ldots N_k(t))$
- Variables: $P_{n_1\ldots n_k}(t)$
- Probability of extinction as a function of time: $P_{0,\ldots 0}(t)$

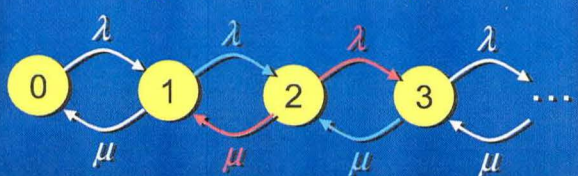
3

Kolmogorov forward equations



4

Kolmogorov forward equations



Rate out = Rate in

$P_2(\lambda+\mu) = \lambda P_1 + \mu P_3$

5

Kolmogorov forward equations

$P_2(\lambda+\mu) = \lambda P_1 + \mu P_3$

Steady state

$P_2'(t) = -(\lambda+\mu)\,P_2(t) + (\lambda P_1(t) + \mu P_3(t))$

Non steady state

6

Kolmogorov forward equations

$$P_{n_1\cdots n_k}(t)' \equiv -\left(\sum_{l=1}^{k} n_l\left(\mu_l(t)+\theta_l(t)\right)+\beta(t)\sum_{l=1}^{k}\sum_{j=1}^{k} n_j\alpha_{jl}(t)\right)P_{n_1\cdots n_k}(t)$$

$$+\beta(t)\sum_{l=1}^{k}\sum_{r=1}^{k}\delta_{[n_l]}n_r\alpha_{rl}(t)\,P_{n_1\cdots n_r\cdots(n_l-1)\cdots n_k}(t)$$

$$+\sum_{l=1}^{k}\sum_{\substack{r=1\\ r\neq l}}^{k}\delta_{[n_l]}(n_r+1)\theta_r(t)\gamma_{rl}(t)P_{n_1\cdots(n_r+1)\cdots(n_l-1)\cdots n_k}(t)$$

$$+\sum_{r=1}^{k}(n_r+1)\theta_r(t)\gamma_{r0}(t)P_{n_1\cdots(n_r+1)\cdots n_k}(t)$$

$$+\sum_{l=1}^{k}(n_l+1)\mu_l(t)\,P_{n_1\cdots(n_l+1)\cdots n_k}(t)$$

for $n_i = 1,\cdots,\infty$, and $i = 1,\cdots,k$, and $\delta_{[a]} = \begin{cases} 1, & a > 0 \\ 0, & a = 0 \end{cases}$

7

Approximation technique

- Number of Kolmogorov forward equations

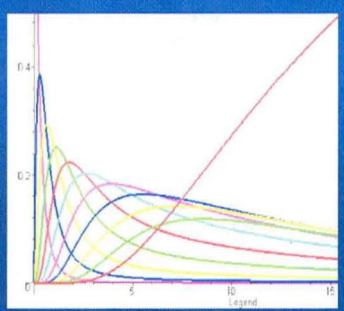
$O(c^k)$

- Number of moment differential equations

$O(k^2)$

8

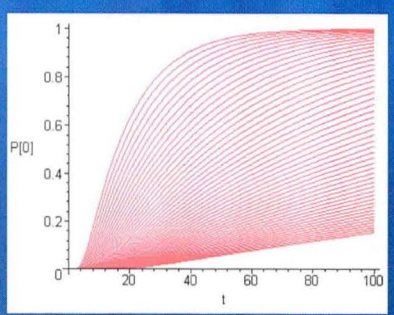
System Behavior



- $P_{0\ldots0}(t)$ inevitably increases over time
- The questicon is how fast

9

System Behavior



10

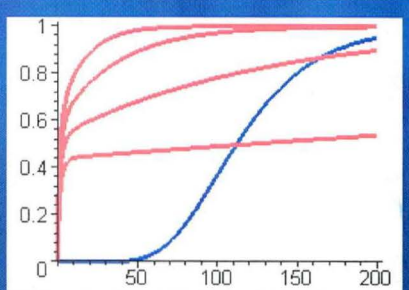
Does abundance matter?

Abundance Model:	Incidence Model:
Moment Matching	Full KF symmetric model

Test: Is there a μ value that gives a similar metapopulation extinction profile?

11

Preliminary Results



12

Preliminary Interpretation

Incidence and abundance models are not giving similar extinction patterns

13

Markov models of endangered species populations and habitat

Laurel Travis, Virginia Tech.
Michael R. Taaffe, Virginia Tech.
Michael Bevers, USDA Forest Service
Curtis H. Flather, USDA Forest Service

14